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MATING BEHAVIORS OF THE BLACKTAIL SHINER, *CYPRINELLA VENUSTA*, FROM SOUTHEASTERN MISSISSIPPI

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Abstract. – I describe reproductive behaviors of *Cyprinella venusta* from the Escatawpa River, George County, Mississippi, using video-tape replays and direct observations of spawning episodes in aquaria. As is typical of members of this genus, *C. venusta* spawns in crevices. During spawning activities, territorial males alternated between defending the crevice, making solo runs along it, and pairing with individual females as they made runs along the crevice. Defense of the crevice involved swift assaults, chases, agonistic displays, and fights. There were two types of fights: lateral-butting and lateral-ramming. The solo runs by the territorial male include the release of sperm into the crevice before oviposition. Small males (sneakers) deposit sperm in the crevice by darting between and disrupting the territorial male and a female making a run long the crevice; and large and small males may make solo runs along a crevice to spawn there when the territorial male is not in the immediate area, both behaviors serving to cuckold the territorial male. The behaviors shown and the frequency with which common behaviors are expressed by members of *Cyprinella* vary interspecifically and may be related to variation in adult size among populations or to phylogenetic factors.

Fishes in the genus *Cyprinella* show a unique spawning mode called "crevice spawning," which may be a synapomorphy (Rabito and Heins, 1985; Mayden, 1989). This phenomenon allows intrasexual competition among males who attempt to monopolize the crevices. The outcome of the competition determines access to reproducing females and thus the reproductive success of the males. The resulting sexual selection has produced a high degree of sexual dimorphism in aggressiveness, body size, and display or combat structures (tubercles) in members of *Cyprinella*. These factors also may have been significant in the evolution of alternative mating tactics in the genus.

Despite the distinctive reproductive mode of *Cyprinella*, there is little information on spawning behavior of these species. Although *Cyprinella venusta* is known to be a crevice spawner (Pflieger, 1975), its spawning behavior has not been studied. Here I describe the mating tactics of the blacktail shiner in aquaria. I also compare the reproductive behavior of *C. venusta* to that observed in other members of *Cyprinella*.

MATERIALS AND METHODS

I collected adult *C. venusta* from the Escatawpa River at County Hwy. 612, George County, Mississippi, on 28 May 1987 and transported them to the laboratory for study. Females (n=14) were 67-80 mm and males (n=10) 75-99 mm standard length (SL). For purposes of this study, small males were 75-78 mm SL (n=2); and large males were 85-99 mm SL (n=8). After observations and video taping had been completed, I examined the gonads of the fish using criteria of Matthews and Heins (1984) and found that all of them were sexually mature.

I kept the fish in a 208-1 aquarium on a 16h light: 8 h dark cycle at about 24° C. I placed a spawning substrate with a crevice, as described in Rabito and Heins (1985), into the aquarium. Descriptions of spawning behaviors were developed from direct observations and replays of video tapes. Based on video tapes alone, I analyzed a total of over 20 hours of spawning behavior; direct observations were not timed.

RESULTS

The different behaviors I describe varied in duration, intensity, and pattern and occurred in varied sequences. Although competitive encounters usually occurred between males of a similar size, they also occurred between males of very different sizes; but the latter occurrences were usually brief, the smaller male withdrawing shortly after the encounter began.

Spawning episodes were orderly to disorderly. At their extreme, disorderly episodes could best be described as a "free-for-all" where spawning fish were massed at the crevice and struggled to get to it; there was little, if any, defense of the resource. The females seemed to force their way through the large number of individuals massed at the crevice, and males sometimes were unable to attend them as they oviposited. Such an event seemed to be due to swamping by non-territorial males who simultaneously approached the crevice; it also may have been due to the presence of a relatively large number of spawning females.

As orderly spawning activities began, a larger (dominant or territorial) male started swimming in the area of the crevice and attempted to exclude other males from access to it. During spawning activities, the dominant male alternated between defending the crevice, making solo runs along it, and pairing with females as they made runs along the crevice. The territorial male defended the crevice by using different agonistic behaviors: "swift assault", "chase", "agnostic display", and "fight". All such encounters occurred within about 0.5 m of the crevice, excepting chases that sometimes extended farther from it. Agonistic encounters occurred among non-territorial males away from the crevice and involved chases, agonistic displays, and fights.

In a swift assault, the dominant male thrusted forward and attempted to ram into another male, usually into his side. The force of the attack often knocked the assaulted male horizontally 90° around his longitudinal axis. A chase occurred when one male pursued a fleeing male beyond the latter's original position. During agonistic displays, males circled head-to-tail

or swam parallel head-to-head with their fins erect and bodies rigid and quivering. Fights were quite variable in intensity and pattern. There were two basic kinds of fights that usually began with a brief agonistic display: lateral-butting fights and lateral-ramming fights. If the males were oriented head-to-tail during the agonistic display, they would circle and butt each other in the side, often in the postero-lateral region of the body, with their snouts. If the males were oriented head-to-head, the fights were more violent; the males rammed head first into each other's side, usually as they swam forward. A male arced out away from a straight-line path and swiftly rammed into the side of his competitor; this knocked the competitor aside horizontally, eliciting a similar attack from him. Thus, the activity of the two combatants often produced a braided pattern of movements. During agonistic displays or fights, males occasionally also bumped each other with their caudal peduncles.

To make a solo run, a dominant male swam up to the crevice. As he began to swim along the opening, he turned horizontally with the ventral surface of the body opposite the crevice. Shortly thereafter he typically began to vibrate the posterior portion of his body which was just opposite, at, or slightly protruding into the crevice. The run along the crevice usually ended when the male turned upward and swam away.

When a female swam into the area of the crevice, the dominant male often orbited around or in front of her or, less frequently, in the area of the crevice. Alternately, the dominant male swam to and followed the female, swimming near, beside, or just slightly behind her. When orbiting, the dominant male swam rapidly in a clockwise or counterclockwise direction. After swimming to the crevice, a female attempting to oviposit turned to swim along it with her ventral surface opposite the opening. The male swam beside and below her along the crevice, sometimes with his head slightly behind that of the female. When ovipositing, a female pivoted suddenly and inserted the vibrating posterior portion of her body into the crevice. The end of one such spawning pass quickly followed when the female exited upward from the crevice with her body arched upward. During the run, the male swam parallel to the female and, after separating from her, usually circled back around to eat eggs that fell out of the crevice.

Large and small, non-territorial males swam up to the crevice and made runs along it when the dominant male was not in the immediate area and could not defend the crevice against intruding males. Additionally, as the dominant male paired with a female and they began to make a spawning pass along the crevice, a small male swimming in the area sometimes swam rapidly to and between the pair to make a brief run along the crevice and quickly swim away. In doing so, he disrupted the paired fish (territorial male and female) causing them to separate and swim away from the crevice.

DISCUSSION

Rabito and Heins (1985) believed there were three possible functions of solo runs along a crevice by a dominant male: crevice testing, courtship display, and deposition of milt. I believe this behavior primarily serves the latter two functions. Runs along a crevice probably attract the attention of females, particularly in nature when visibility is not likely so good, and thus show them where a suitable crevice is guarded by a male ready to spawn. Emission of milt is not visible in species of *Cyprinella*, and direct evidence of milt release is not available. However, several lines of evidence suggest that solo runs along a crevice involve emission of sperm. First, the orientation of a male's vent in relation to the crevice and the vibration of his body when making a solo run indicate that sperm are being emitted into the crevice; females show similar behavior when ovipositing. Second, when a male is paired with a female along a crevice as she oviposits, there seems to be little, if any, opportunity for the deposition of sperm because the male's vent is not very close to the crevice. Third, other males, both large and small, exhibit similar behavior in making runs along the crevice when the dominant male is unable to defend it. Fourth, my observations suggest that during disorderly spawning episodes a female may oviposit without pairing with a male.

The behavior of small males in response to a spawning pair represents sneaky behavior (Gross, 1984) and is the first published description of this alternative male reproductive tactic in the genus *Cyprinella*; however, Ferguson (Abstract, ASB Bulletin 36: 66) has reported sneaky males in *Cyprinella trichroistia*. Solo runs along a crevice by non-territorial males (large and small) in the absence of the dominant male appear to have the same effect of cuckolding the dominant male. Thus, this behavior should be considered an alternative mating behavior unique to crevice-spawning, male *Cyprinella*.

I propose the following hypothesis of events involved in the spawning of *C. venusta*. While defending a spawning territory around a crevice through agonistic interactions with other males, a territorial male releases sperm into a crevice as he makes solo runs along it, also signaling to females nearby that he is ready for them to oviposit in the crevice he guards. The eggs of females that oviposit in the crevice are fertilized by sperm present there. Small males take advantage of a situation where the dominant male is attending a female and is unable to guard the crevice. Thus, by darting between the paired fish and disrupting the spawning pass, small males sneak opportunities to deposit sperm in the crevice and gain fertilizations of eggs. Large and small males also may gain fertilizations by depositing sperm in crevices when the territorial male is not in the immediate area.

Variation in the repertoires of members of *Cyprinella* appear to involve differences in the behaviors that are shown and in the frequency with which common behaviors are expressed. The interspecific variation may be related to differences in adult size among populations or to phylogenetic factors.

Some behaviors may occur only in particular species or species groups. Swift assaults have not been described for the genus heretofore and may be unique to *C. venusta*. Similarly, pelvic and anal fin grasps have been reported only for *C. spiloptera* (Gale and Gale, 1977). As discussed above, sneaky behavior has been reported for only two *Cyprinella* to date. Likewise, use of a crevice by males when the territorial male was not in the immediate area has been observed in only one other member of the genus, *C. callitaenia* (Wallace and Ramsey, 1981). Although some behaviors may be limited to certain species, others may be shared by many, if not all, species of *Cyprinella*. Agonistic displays, chases, and fights are shown in a number of species (Outten, 1958; Pflieger, 1965;

Stout, 1975; Gale and Gale, 1977; Rabito and Heins, 1985).The agonistic behavior of *C. venusta* seems to be typified by a higher degree of violent encounters with conspecific males than in other *Cyprinella*. For example, males of *C. leedsi* mostly exhibit "mock battles" (extended agonistic displays and lateral-butting fights), chases, and threat displays (Rabito and Heins, 1985); but the larger *C. venusta* often showed swift attacks, fights and chases. Swift attacks were not observed for *C. leedsi*, and *C. venusta* spent relatively little time engaging in agonistic displays (Heins, pers. obser.). In addition, fights described for other species generally seem to involve lateral butting (Pflieger, 1965; Stout, 1975; Rabito and Heins, 1985) rather than the more violent lateral-ramming fights that I also observed for *C. venusta*.

Comparisons of behaviors in *Cyprinella* are tentative because variable treatments in earlier reports do not always allow direct comparison. In some cases, behaviors were named but not described. In others, descriptions of behaviors lack the details necessary to be certain of their identity. Furthermore, observations have been made for only a small number of species in the genus.

To summarize, I have described reproductive behaviors in *C. venusta*, including alternative mating tactics among males. Alternative mating tactics in *C. venusta* arise from sexual selection based on its crevice spawning mode. Dominant, territorial males sequester and defend presumably limited spawning crevices in nature (Pflieger, 1965) through primary tactics involving aggressive, sometimes violent, competition to monopolize access to females. Large (non-territorial) and small males use alternative tactics to gain fertilizations of eggs. Both large and small males will spawn in a crevice when the territorial male is not in the immediate area. Small, sneaky males dart between the territorial male and a female making a spawning run along the crevice.

ACKNOWLEDGEMENTS

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MINUTES

Business Meeting
15th Annual Meeting
Southeastern Fishes Council

The Southeastern Fishes Council met at Charlotte, N.C. in the Welwyn Room of the Hilton at University Place on April 7, 1989. Chairman Robert E. Jenkins presided. The meeting was called to order at approximately 5:04 pm local time.

Secretary's Report: The Minutes of the 1988 meeting appeared in the *PROCEEDINGS*. The Minutes were approved without correction.

Treasurer's Report:

		Balance
Checking Account (1-31-89)		$1,371.55
1989 dues received (3-31-89)	380.00	
Cost of Issue No. 18	(310.31)	
Checking Account Balance (3-31-89		1441.24
Paine Webber Cash Fund (2-24-89)		1761.31
TOTAL ASSETS (4-1-89)		$3202.55